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How a System of Checks on Symbiosis Could Become Disastrous

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Corals are small marine invertebrates that band together to create the world's largest animal engineered structures: the coral reef. Some of these reef structures such as The Great Barrier Reef in Australia are so large they can be seen from the International Space Station. Often referred to as the Amazon Rainforests of the ocean, coral reefs support a diverse array of marine ecosystems and harbor much of the oceans biodiversity. Recently, corals have gained global attention due to a massive global die off event in 2016, in which almost 30% of all corals on the Great Barrier Reef died.[1] Before this massive reef die off many of the corals underwent a process called coral bleaching in which the coral animal expels its photosynthetic symbiont, a dinoflagellate of the genus *Symbiodinium*, into the surrounding water revealing a ghost-like white skeleton. Corals receive most of their required nutrients from their *Symbiodinium* partner in the form of photosynthetically fixed carbon therefore after *Symbiodinium* expulsion the coral animal is physiologically weak and vulnerable to disease.[2] Despite this sensitive coral-*Symbiodinium* partnership, corals have been around for 10–100 s of millions of years begging the question why has not a more robust relationship evolved?

In the current issue, Blackstone and Golladay[3] address this fundamental question, "Why do corals bleach?" They propose that bleaching is caused by a breakdown of the mechanisms that mediate conflict between corals and their symbionts. A mechanism of conflict mediation in this case is a means to check if the *Symbiodinium* partner is conforming to a particular behavior, which is to export photosynthate to the coral. Blackstone and Golladay focus on how the breakdown of two mechanisms co-opted from features of photosynthesis can lead to bleaching. The first is end-product inhibition caused by the buildup of fixed carbon by the *Symbiodinium*. The second is a breakdown of the coral's carbon-concentrating mechanism, which causes a shortage of CO_2 to be fixed by the *Symbiodinium*. The authors discuss that when either mechanism is irregular, the redox state of the NADP $\pm$ NADPH pool shifts towards a reduced state causing electrons to be backed up on photosystem I and II. The overabundance of electrons results in more frequent transfer to molecular oxygen, forming reactive oxygen species (ROS). When ROS builds up in excess programmed cell death can occur at an elevated rate.

Along with the growing appreciation of how symbiosis fits within the model of multiple levels of selection, Blackstone and Golladay examine these mechanisms in a larger evolutionary framework. This has yielded predictions of how an unchecked mutualistic symbiosis between coral and Symbiodinium may degenerate into a parasitic one. To evaluate how failures of conflict mediation may lead to this, the authors propose experiments that target functional gene markers, such as transporters, that may be involved in the export of photosynthate from Symbiodinium to coral. Loss of function mutations in transporter associated genes might be a signature of defector symbionts. In addition, it would be beneficial to understand any other genotypic links to the cheater symbiont phenotype, perhaps in regulatory networks. Finally, the authors discuss how redox state, measured in situ via microscopic techniques, while challenging, could be used to determine instances in which ROS formation may be elevated. Recent advances in underwater microscopy could further aid in localizing the emergence of cheater symbionts in situ.[4]

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